Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

SOME RELATIONS BETWEEN ANTS AND FUNGI

IRVING W. BAILEY

Bussey Institution, Harvard University

The remarkable fungus-growing and fungus-feeding habits of the neotropical Attiine ants, first surmised by Belt (1874) and Fritz Müller (1874) and subsequently elucidated by the classical investigations of Tanner (1892), Alfred Moeller (1893), Huber (1905) and Wheeler (1907), have led to a search for other fungivorous representatives of the Formicidæ.

Emery (1899) is of the opinion that *Messor barbarus* subsp. *structor* Latr. feeds upon fungi, as well as seeds and other food-substances. Lagerheim (1900) states that *Lasius fuliginosus* Latr. cultivates *Cladotrichum myrmecophilum* (Fres.) Lag.,[1] which functions as a food and in giving stability to the walls of its carton nest. Ferdinandsen and Winge (1908) quote Raunkiaer as having reached the conclusion that *Chromosporium formicarum* Ferd. & Wge. is eaten by the ants in whose nest it grows. Farquharson (1914) appears to favor the view that certain Nigerian Crematogasters are fungus-farmers. Donisthorpe (1915) believes that *Cladosporium myrmecophilum* (Fres.) Ell. is an important item of food in the diet of *Lasius fuliginosus,* and that *Hormiscium pithyophilum* (Wallr.) Saccr. var. *myrmecophilum* Ell. is cultivated by *L. umbratus* Nyl. Elliott (1914) suggests that the "pure cultures" of fungi in the carton nests of *L. fuliginosus* and *L. umbratus* probably originate—as is the case with fungi cultivated by certain Attiine ants—by a transfer of a definite culture of mycelium which is subsequently manured, tended and weeded by the ants.

The principal arguments advanced in favor of the view that various Formicidæ, other than the Attii, cultivate and feed upon fungi are the following: (1) The association of a particular fungus with a particular species of ant, (2) the occurrence of the fungus in "pure cultures," (3) the cropping of aerial and other hyphæ by the workers and, (4) analogies with the fungus-growing and fungus-feeding habits of the Attiine ants. It is to be emphasized in this connection, however, that the occurrence of more or less pure cultures of a particular fungus in the domatia of a given species of insect, does not indicate necessarily that the mycelium is actually cultivated and eaten by the latter, since, as suggested by Perkins (1914), the mats of hyphæ may be adventitious. Nor is the cropping of aerial hyphæ conclusive evidence that a fungus is eaten by an insect. Miehe (1911) found localized, luxuriant growths of certain fungi in the pseudo-bulbs of the myrmecophytic Hydnophytum and Myrmecodia, but concluded that the aerial hyphæ are cropped by the ants merely to prevent them from obstructing the galleries. Furthermore, it must be admitted that there is a considerable element of uncertainty in reasoning, from analogy with the highly specialized, phytophagous Attii, that representatives of the cosmopolitan, more or less omnivorous Crematogastrii, Formicii, etc., are fungus farmers.

---

[1] Elliott (1914) considers that this fungus is not a *Cladotrichum* and refers it to *Cladosporium myrmecophilum* (Fres.) Ell.

Relations between Ants and Fungi in Myrmecophytes

Recently, I have devoted considerable attention to the study of an interesting group of African myrmecophytes.[2] These ant-inhabited plants, which belong to three distinct orders, Parietales, Tubifloræ and Rubiales, are characterized by an inherent tendency towards the formation of a heterogeneous pith, the central succulent portion of which collapses and dries up, leaving an internal chamber or cavity which is taken possession of by ants and used as a domatium. In certain of the Ethiopian myrmecophytes, species of Cuviera, Plectronia and Sarcocephalus and *Barteria fistulosa* Masters, the internal cavities tend to be localized in certain shoots or particular portions of the stems and branches, and are concomitants of more or less pronounced hypertrophies of these organs; whereas in others, *Vitex Staudtii* Guerke and *Barteria Dewevrei* De Wildeman & Durand, the phenomenon is less localized and there are no external indications of swellings or enlargements of the stems and branches. All of the myrmecophytes differ from previously described extra-African myrmecophytic plants in the occurrence within their myrmecodomatia of excavations which contain peculiar callus-heteroplasias. These traumatic structures, zoöcecidia, are arranged more or less symmetrically in relation to the phyllotaxy of the plants, and are formed by the young cambium and cortex when these tissues are exposed by the removal of the underlying cells of the medulla and xylem. In endeavoring to trace the various stages in the development of the zoöcecidia, and to account for their symmetrical distribution in relation to phyllotaxy, I have had occasion to section a considerable number of myrmecodomatia and to study the minute anatomy of various extra-Ethiopian myrmecophytes for purposes of comparison.

All of the ant-inhabited plants (species of Acacia, Triplaris, Cecropia, Nauclea, Enterolobium, Myrmecodia and Hydnophytum, as well as Cuviera, Vitex, Plectronia, Barteria and Sarcocephalus) of which I have succeeded in obtaining suitable material[3] have a more or less luxuriant growth of fungi upon the inner walls of their myrmecodomatia. The mycelia are sporadically distributed in most cases, but their aerial portions show unmistakable evidences of having been cropped by the ants. In three of the myrmecophytes, *Plectronia Laurentii* De Wildeman[4] and *Cuviera angolensis*[4] Hiern. and undetermined material of the latter genus[5] there are dense mats of delicate, white hyphæ which resemble "ambrosia." These mycelia are confined to the two concave ends of the spindle-shaped domatia. As shown in figure 1, the aerial hyphæ project from a dark colored substratum which rests, in turn, upon medullary tissue. When macerated, the dark colored layer is found to be composed of the detritus of the ant colony, *i.e.*, fecal substances, disintegrated pellets, etc. The mycelium radiates through this detritus in all directions and penetrates into the superficial layer of medullary cells.

---

[2] Bailey, I. W., "The Anatomy of Certain Plants from the Belgian Congo, with Special Reference to Myrmecophytism," Bull. Am. Mus. Nat. Hist. Ined.

[3] The bulk of the material consisted of freshly killed speimens preserved in 70–90 percent alcohol.

The questions suggest themselves, accordingly, (1) are the mycelia, which occur in the various myrmecodomatia and are cropped by the ants, eaten by them, and (2) are they cultivated by the ants or merely adventitious?

Of course, there are serious obstacles in the way of securing observations upon the normal activities of ants in myrmecophytes, even when living plants and insects are available. In dealing with other groups of animals, under somewhat similar circumstances, investigators have resorted to analyses of feces or the contents of alimentary tracts. Although ants are supposed to take only fluid or semifluid substances into their crops and stomachs, they have a curious infrabuccal chamber, into which pass fragments of animal and plant tissues upon which they are feeding. The material that accumulates in this cavity—in the form of a pellet—is finally cast out or fed to a larva (Pseudomyrminæ).

A number of the pellets of the Crematogasters which inhabit the myrmecophytic Cuvieras are composed entirely of fragments of the ambrosia-like mycelia (fig. 2). Furthermore, the infrabuccal chambers of the ants[6] which inhabit the other myrmecophytes contain numerous fragments of aerial hyphæ (fig. 4), which appear to have been removed from the walls of the domatia. Although such facts as these might be considered to indicate that the ants feed to a greater or less extent upon the fungi, they afford no clue in regard to our second question. There are, however, certain general phenomena which are worth recording in this connection.

The environment in the interior of the myrmecodomatia is usually very favorable to the growth of fungi. The walls of the domatia are commonly excellent "culture-media" and the equable temperatures of the moist, dark chambers facilitate the germination of spores and the growth of mycelia.

---

[4] Inhabited by *Crematogaster africana* subsp. *laurenti* var. *zeta* Forel.

[5] Inhabited by *C. impressiceps* var. *frontalis* Santschi (var. nov.).

[6] Species of *Pachysima, Pseudomyrma, Azteca, Viticicola, Crematogaster* and *Camponotus*.

Under these circumstances, it is almost inevitable that the nests should become infected with fungi; for not only do the ants transport spores, which become accidentally attached to their bodies and appendages, but their pellets contain numerous spores[7] of different kinds, the most resistant types of which probably remain viable. The growth and sporadic distribution of the hyphæ in most of the myrmecodomatia suggest that the mycelia are purely adventitious. Only in the case of the localized luxuriant growths of "ambrosia" in *Cuviera* and *Plectronia* are there indications that the ants may actually be fungus-farmers; *i.e.,* the mycelia appear to me more or less pure cultures and are closely associated with the detritus of the ant colonies.

Von Ihering (1898) and Huber (1905) have shown that the *Atta* queen, during her nuptial flight, carries a culture of mycelium in her infrabuccal sac, which is deposited in the new nest, fertilized with liquid feces and triturated eggs, and carefully tended first by the queen and subsequently by the incipient colony. The walls of recently occupied myrmecodomatia of *Cuviera* are covered with aerial hyphæ (fig. 3). As the colony increases in size, the walls are scarified and the hyphæ cut away except at the ends of the domatia, where the detritus of the colony is deposited and the future "fungus-gardens" are located. It is conceivable, therefore, that the luxuriant growths of ambrosia may have originated in one of the following ways: (1) By the adventitious growth of some ubiquitous fungus which, in the peculiar environmental conditions within the myrmecodomatium, tends to become dominant and is finally confined to those portions of the nest where the detritus of the colony is deposited; (2) by a process of selective weeding on the part of the ants; (3) by the transfer of a definite culture of a particular fungus which tends to diffuse over the walls of the domatium until it can be confined, manured and weeded by the developing colony. It does not seem probable, however, that the facultative and more or less omnivorous Crematogasters have attained as high a degree of specialization in their relation with fungi as is essential if the latter solution is the correct one. Furthermore, it should be noted that frequently there is a tendency among ants to deposit their feces, the castings from their infrabuccal cavities, etc., in some more or less restricted portion of their domatia. These aggregations of partly digested animal and plant tissues naturally tend to give rise to luxuriant growths of fungi. Therefore, the fact that the dense mats of ambrosia rest upon detritus cannot be considered, in the absence of reliable collateral evidence, to indicate necessarily that the myeclia are actually manured and tended by the ants.

---

[7] Many of the pellets contain, in addition to fragments of fungi and other substances secured from within the myrmecodomatia, much extraneous material, i.e. fragments of insects, bits of plant tissue, hairs, pollen, dirt, and large numbers of spores of many different kinds, fig. 5.

Relations between Other Formicidæ and Fungi

The occurrence of large numbers of spores and fragments of hyphæ in the pellets of certain Pseudomyrminæ, Myrmicinæ, Dolichoderinæ and Formicinæ, which are "obligatory" or "facultative" inhabitants of various Ethiopian and extra-African myrmecophytes, raises the question, is this relation between ants and fungi an isolated phenomenon or one that is characteristic of other representatives of these subfamilies?

Pseudomyrminæ.—The strongly hypocephalic larvæ of Pseudomyrmine ants[8] are fed with pellets voided from the infrabuccal pockets of the workers. The pellets are inserted into a curious depression or pouch (trophothylax) which is located on the ventral surface of the larva close to its head. Owing to their relatively large size and dark color, these pellets are quite conspicuous and easily obtained from larvæ preserved in alcohol. My colleague, Professor W. M. Wheeler,[9] and I have recently analyzed more than 400 pellets of various Pseudomyrminæ. The larvæ, from which the pellets were taken, belonged to a number of different species and varieties of the four genera of this subfamily, and were collected at various seasons of the year in several localities in Texas, Mexico, Guatemala, Costa Rica, British Guiana, the West Indies, the Philippines and the Belgian Congo. As was to have been expected, *a priori,* in view of the well-known entomophagous habits of these ants, 85 percent of the pellets contain more or less numerous fragments of insects, *e.g.,* coccids, mites, spiders, beetles, larvæ, etc. (fig. 6). Although a number of these pellets, approximately 25 percent, are composed entirely of animal tissue, a majority, 65 percent, contain fungous spores and fragments of hyphaæ (fig. 9). Frequently the spores and hyphæ are so numerous as to form a large fraction of the total volume of the pellet. Furthermore, many of the pellets, which are devoid of animal tissue, are composed entirely of spores (fig. 8), or spores mixed with pollen (fig. 7). Usually the spores are of several distinct types (figs. 7, 11), but occasionally a pellet is encountered in which they are all, or nearly all, of one variety (fig. 8). The fungus-containing pellets are not confined to any particular groups of the Pseudomyrminæ, but occur in all species and varieties, regardless of the locality where they were collected or the nesting habits[10] of the ants.

The infrabuccal pockets of imagines, queens and workers contain the same assortment of substances as the larval trophothylaces, but usually in somewhat different proportions. In other words, they tend to have a smaller proportion of animal tissue. This is due, in all probability, to the fact that the worker-nurses add fragments of insects to their pellets before feeding them to the larvæ.

---

[8] *Pseudomyrma, Pachysima, Tetraponera,* and *Viticicola.*

[9] Wheeler, W. M., and Bailey, I. W., "The Feeding Habits of Pseudomyrmine and other Ants," Trans. Amer. Phil. Soc. Ined.

[10] Nesting in the ground (*Pseudomyrma elegans* Sm.), in dead twigs (*Tetraponera, Pseudomyrma*) or in myrmecophytes (*Pseudomyrma, Pachysima, Viticicola*).

PONERINÆ, DORYLINÆ, MYRMICINÆ, DOLICHODERINÆ, AND FORMICINÆ.—More recently, the writer has dissected the heads of queens, males, soldiers and workers of various representatives of the Ponerinæ, Dorylinæ, Myrmicinæ, Dolichoderinæ and Formicinæ, and studied the contents of their infrabuccal cavities. The results of analyses of 736 pellets from 25 genera of the five subfamilies are recorded in the following table:

PONERINÆ

Ant	Locality	Nesting in	Food			
			Animal tissue	Plant tissue	Fungi	No pellets
Myrmecia tarsata Sm.	N. S. W.	Ground	S	A	F–VN	14
M. gulosa Fabr.	N. S. W.	Ground	S–A	A	N–VN	8
Paraponera clavata Fabr.	Panama	Ground	S	A	VN	10
Diacamma australe Fabr.	Queensland	Ground	S	A	VN	16
Odontomachus hæmatoda L.	Costa Rica	Ground	S	A	N–VN	10
DORYLINÆ						
Dorylus anomma var. *nigricans* Illiger	Congo	Ground	A	?	F	18
Eciton burchelli Westwood	British Guiana	Ground	A	S	F–N	10
MYRMICINÆ						
Leptothorax curvispinosus Mayr	N. Y.	Dead twigs	?	A	N	41
Aphænogaster tennessensis Mahr.	Mo.	Rotten stumps and logs	?	A	N	30
Veramessor pergandei Mayr	Ariz.	Ground (H)	?	A	F	18
V. andrei Mayr	Calif.	Ground (H)	?	A	F	12
Pogonomyrmex barbatus Sm. var. *marfensis* Wheeler	Texas	Ground (H)	S	A	F–N	46
P. barbatus Sm. subsp. *rugosus* Em.	Ariz.	Ground (H)	S	A	F–N	42
Solenopsis geminata var. *rufa* Jerdon	P. I.	Ground (H)	?	A	N	6
S. geminata var. *diabola* Wheeler	Texas	Ground (H)	?	A	F–N	18
Myrmicaria eumenoides Gerst.	Congo	Ground	?	A	F–VN	12
Atta cephalotes L.	(3) Costa Rica	Ground	?	A	F–VN	22
Trachymyrmex septentrionalis McCook var. *obscurior* Wheeler	Florida	Ground	?	A	F–N	8
Cryptocerus multispinus Em.	Guatemala	Dead branches	S	A	F–VN	8
DOLICHODERINÆ						
Liometopum apiculatum Mayr	Ariz.	Carton nests in hollow live oaks	?	A	F–N	10
L. occidentale Em.	Calif.	Carton nests in hollow live oaks	S–A	A	N–VN	18
Leptomyrmex nigriventris Guérin	N. S. W.	Hollow logs	S	A	N–VN	14
Dolichoderus doriæ Em.	N. S. W.	Ground	S–A	A	F–VN	19
Azteca instabilis Sm.	Guatemala	Carton nest	S	A	VN	24

FORMICINÆ

Ant.	Locality	Nesting in	Food			
			Animal tissue	Plant tissue	Fungi	No. pellets
Œcophylla longinoda Fabr.	Congo	Silk and leaf nests on trees	S	A	N	16
Lasius fuliginosus Latr.	Switzerland	Carton nests hollow trees	?	S	VN	33
L. interlectus Mayr	Ill. and Colo.	Ground	?	A	F–N	12
Formica rufa L. var. *obscuripes* Forel	B. C.	Mound nests	?	A	F–VN	17
Myrmecocystus melliger Forel	N. Mex.	Ground	?	A	F	12
Camponotus maculatus Fabr. subsp. *McCooki* Forel var. *sansabeanus* Buckley	Texas	Ground	A	S	F–N	11
C. brutus Forel	(3) Congo	Rotten wood	S	A	VN	50
C. sericeiventris Guérin	Guatemala	Rotten tree trunks	?	A	VN	35
C. acutirostris Wheeler	Ariz.	Ground	S–A	A	F	7
C. herculeanus L. subsp. *ligniperda* Latr. var. *novaboracensis* Fitch.	(2) N. Y.	Decaying stumps	S	A	N	41
C. abdominalis Fabr. var. *costaricensis* Forel	Costa Rica	Dead trees	S	A	N–VN	17
C. nigriceps Sm.	Queensland	Ground	A	A	F–VN	18
Polyrhachis dives Sm.	P. I.	Silk and detritus nests on trees	A	A	F–VN	10
P. ammon Fabr.	N. S. W.	Ground	S–A	A	F–VN	23

S = fragments of tissue scanty.
A = fragments of tissue abundant.
F = spores or fragments of hyphæ infrequent.
N = spores or fragments of hyphæ numerous.
VN = spores or fragments of hyphæ forming considerable fraction of total volume of pellet.
H = seed-storing ants.

It is significant that fragments of insects, such as are present in the infrabuccal sacs of Pseudomyrminæ, are of infrequent occurrence except in the pellets of Dorylinæ, *Myrmecia gulosa, Liometopum occidentale, Dolichoderus doricæ Camponotus maculatus* var. *sansabeanus, C. acutirostris, C. nigriceps* and *Polyrhachis.* On the other hand, vegetable substances are almost invariably present except in the Dorylinæ.

The pellets tend to contain more or less numerous spores and fragments of hyphæ. This is as true of the supposedly primitive, entomophagous Ponerinæ as of the more or less omnivorous Myrmicinæ, Dolichoderinæ and Formicinæ; of ants of temperate as of tropical regions; and of species which nest in the ground or in carton or silk domatia, as of those which live in decaying plant tissue. As shown in the sixth column of the table and in Plate VI many of the ants have pellets that contain large numbers of spores—usually of several (3–12) distinct types—and numerous fragments of hyphæ. Occasionally a pellet is encountered which is composed entirely of fungus filaments and spores, but usually there are present at least a few bits of sound or decaying plant tissue. I have found very few pellets that are entirely devoid of fungi, except among the Dorylinæ, Veramessor, Pogonomyrmex, Myrmecocystus and *Camponotus maculatus* var. *sansabeanus.* However, even the harvesting ants, which live in relatively xerophytic environments, frequently have numerous spores and bits of chromogenic hyphæ in their infrabuccal chambers.

It is evident, accordingly, that there is a general tendency among ants for the imagines to take spores and fragments of myeclia, or bits of decaying plant tissue, into their infrabuccal pockets. What then is the significance of this generalization? Are most Formicidæ fungivorous? The answer to these questions depends upon the function of the infrabuccal chamber, whether it is actually a receptable for nutritive material or a sort of cephalic dustpan for accumulations of food-residues and detritus.

Structure and Function of the Infrabuccal Cavity

The infrabuccal cavity of wasps was studied by Brants (1841), who came to the conclusion that it functions as a receptacle for materials used in the construction of carton. This supposition was criticised by Meinert (1860). He was inclined to believe that the "mouth-sac" of ants and wasps serve as a crop or "social stomach." Adlerz (1886) rejected Meinert's explanation, but offered no substitute hypothesis. Lubbock (1877) devoted considerable attention to the study of the anatomy of the mouth-sac. He states:

> "In the posterior wall of the mouth is an orifice which leads into a large lobular sac. . . . Its membranous walls appear to be firm and elastic. I have not found any muscles attached to it, and presume that it is kept open by the elasticity of the walls. The orifice of the mouth sac can be closed at will by a small flap which is supplied with several muscular fascicles. The cavity generally contains a brown, spongy mass. . . . In ants, as it seems to me, the general action of the muscles which open the pharynx would tend to empty the mouth sac; those which draw down the lower wall of the pharynx, by directly constricting the mouth sac, while even those attached to the upper wall of the pharynx would tend to empty the mouth sac by sucking out its contents. . . . In fact, as it seems to me, the contents of the mouth sac are not intended only to pass outwards through the mouth, but, on the contrary, into the œsophagus through the pharynx."

Janet (1895*a*, 1895*b*, 1896, 1897) appears to be the only student of ants who has studied the function of the infrabuccal sac with any degree of care. He endeavored to prove, by feeding experiments in artificial nests and by dusting ants with various powders, that the infrabuccal pellets are composed either of food-residues or dust and detritus (which the imagines remove by means of their toilet-organs from their own bodies, from their progeny and from their companions) or a mixture of these two classes of substances.

"Au-dessus du labium il y a une cavité supralabiale, de forme arrondie, dans laquelle les matières pulpeuses râpées, plus ou moins comprimées, abandonnent les liquides qui sont absorbés comme nourriture et laissent, comme résidus, les parties solides trop grossières qui sont rejetées moulées en petits corpuscules enroulés de forme caractéristique. Il suffit de donner, par exemple à des *Lasius fuliginosus* que l'on vient d'installer dans un nid artificiel, une mangeoire garnie d'un mélange de miel et d'amidon pour trouver, quelques heures après, tout autour de la mangeoire, un bon nombre de ces petits corpuscules. C'est au-dessus de cette cavité de moulage des déchets et détritus solides que se trouve l'orifice buccal proprement dit" (1896, p. 15).

Si l'on saupoudre des Fourmis (*Myrmica*) avec du tournesol bleu en poudre fine, elles s'en débarrassent assez vite. On constate d'abord qu'elles circulent pendant quelques instants dans la boîte sans faire aucune tentative de nettoyage. Mais bientôt elles font passer leurs antennes dans l'organe pectiné, puis elles nettoient ce dernier en faisant passer leurs pattes entre les mandibules et les mâchoires. Au bout de quelques heures, on retrouve cette substance sous forme de petits grains, bleus, assez lisses et légèrement adhérents au verre. . . . Les Fourmis grattent avec leurs mandibules le gypse coloré en rouge qui constitue leur nid et elles se salissent avec la poussière ainsi produite. On retrouve, dans ce cas, le produit du nettoyage de leur corps sous forme de grains semblables aux précédents, mais rouges et granuleux (1895*a*, p. 697).

"Comme les Fourmis, le Frelon nettoie ses antennes et d'autres parties de son corps avec ses peignes tibio-tarsiens. Les détritus ainsi enlevés sont repris par les peignes du promuscis et, finalement, emmagasinés dans la cavité supralabiale où il est rare de n'en pas trouver une petite quantité. Ils restent là et s'accumulent, jusqu'au moment où ils seront rejetés, comme partie intégrante d'un corpuscule enroulé. On peut voir les Frelons rejeter un semblable corpuscule presque chaque fois qu'ils terminent un repas sur du miel granuleux. Ils avalent la partie liquide et emmagasienent, dans leur cavité supralabiale, les granulations solides" (1895*b*, p. 108).

In dissecting queens, males, soldiers and workers of various representatives of the Ponerinæ, Dorylinæ, Pseudomyrminæ, Myrmicinæ, Dolichoderinæ and Formicinæ, and removing their pellets, I have had the opportunity of studying the anatomy of the infrabuccal pocket and its relation to other organs and tissues in the imaginal head. There appears to be no system of muscles or other visible mechanism for actually crushing, grinding or expressing liquids from the infrabuccal pocket. Furthermore, there are no glands which feed directly into it. If it is periodically flooded with granular secretions, they must drain or be forced into it from the pharynx or labium. There is no evidence, however, to indicate that the ants are able to digest any considerable portion of the more or less finely divided solid substances that are taken into the infrabuccal sac. The cells in voided pellets still retain their contents (starch, protoplasm, nuclei, etc.) and do not appear to have been acted upon by secretions from salivary or other glands. In fact, my observations favor Janet's contention that the function of the sac is to serve as a receptable for food-residues and detritus; or at least may be explained most satisfactorily upon the basis of such an assumption. Thus, the pellets of ants which nest in or travel over the ground contain much mineral matter, sand, dirt, etc. (fig. 13). On the other hand, the pellets of ants which excavate in sound or decaying twigs, stems, logs, stumps or roots, or utilize malaxated plant tissues in the construction of mounds or carton nests, have a relatively large admixture of vegetable débris. For example, as shown in figure 14, the pellets of *Camponotus herculeanus* subsp. *ligniperda* var. *novaboracensis* are composed principally of fragments of the thick-walled, heavily lignified tracheids and ray-parenchyma of *Thuja occidentalis* L. The infrabuccal sacs of *Leptothorax curvispinosus, Aphænogaster tennesseensis, Camponotus brutus, C. sericeiventris,* and *C. abdominalis* var. *costaricensis* usually are more or less completely filled with fragments of the moribund plant tissues in which the galleries and domatia of these ants are excavated. In a similar manner, the pellets of *Azteca xanthochroa, Pachysima æthiops, P. latifrons, Viticicola tessmanni*, and various species of *Crematogaster* and *Pseudomyrma* which inhabit myrmecophytes, contain a large admixture of triturated medullary and other tissues from the scarified walls of their domatia. When an ant has eaten or dismembered an insect, the infrabuccal sac tends to contain bits of chitin, hairs, scales, mandibles, tracheæ, etc., but few fragments of softer and more nutritious tissues.

That the infrabuccal cavity does not function as a receptacle for food, which is to be acted upon by saliva and other glandular secretions, is indicated, furthermore, by the composition of the pellets of the Attiine and seed-storing ants. Although the former are known to feed upon "kohlrabi" or "bromatia," and the latter large upon seeds, the infrabuccal pellets (that I have analyzed) seldom contain any considerable quantity of these food substances. The pellets of the Attii are composed largely of dirt, plant and animal hairs, bits of epidermal and other plant tissues, fragments of chromogenic hyphæ, spores, pollen, etc. (fig. 12); those of the harvesting ants largely of sand (fig. 13), dirt, bits of seed-coats, husks and other resistent plant tissues, fragments of dark-colored hyphæ, spores, hairs, etc. Occasionally, the infrabuccal chambers of the harvesting ants contain large fragments of seeds, but none of the pellets of the Attii that I have analyzed contain more than a few small bits of delicate, white hyphæ. It is of interest, in this connection, that the investigations of Moggridge (1873), Emery (1912) and others indicate that the harvesting ants feed upon the non-starchy, fluid or easily soluble portions of seeds.

ARE THE FUNGI IN THE INFRABUCCAL SAC FOOD-RESIDUES OR DETRITUS?

The consensus of opinion among students of ants is that these insects do not masticate their food with their mandibles or maxillæ. The act of feeding consists in lapping or rasping nutrient substances with the roughened surface of the protrusible tongue. However, the mandibles are used in tearing the food into pieces of convenient sizes and in rendering available its softer and more nutritious portions. Thus, the infrabuccal sac may contain, in addition to detritus of different kinds and from different sources, two distinct types of food-residues: (1) coarse fragments, which adhere to the surfaces of the ants during the process of cutting up or dismembering the food, and (2) finely divided particles, rasped off by the tongue and segregated from the fluid or semifluid substances that pass into the crop.

My analyses show that the crops and stomachs of the imaginal ants do not contain spores or fragments of hyphæ. If the ants actually feed upon fungi, they must triturate the spores and mycelia, or compress them, and drain off their liquid or semiliquid contents. Under such circumstances, one should expect to find torn or ruptured spores and finely divided fragments of hyphæ in the infrabuccal cavity. This is not the case, however, in any of the pellets that I have analyzed. The spores and the fungus filaments still retain their protoplasmic contents. In fact, all of the evidence at hand indicates that they are detritus scraped from the bodies and appendages of the ants, rather than food-residues. This is true even in the case of *Lasius fuliginosus, Crematogaster africana,* subsp. *laurenti* var. *zeta,* and *C. impressiceps* var. *frontalis,* in whose domatia are found what appear to be "pure cultures" of particular fungi.

The structure and activities of ants are such that they inevitably must accumulate numerous spores upon the hairy surfaces of their bodies and appendages, just as they do dirt, pollen and other types of detritus. In addition, the environmental conditions within their domatia facilitate adventitious growths of fungi which must be kept within bounds by a constant cropping of the mycelia. Luxuriant growth of aerial hyphæ, if they do not actually occlude the galleries and domatia, form formidable entaglements, and are likely to interfere with the brood. Thus, small colonies of ants in artificial nests frequently are swamped by fungi whose rapid growth cannot be controlled by a limited number of workers. In scarifying, cleaning and smoothing the walls of their domatia, ants become covered with bits of excavated materials (mineral or vegetable) and fragments of hyphæ, a considerable portion of which are swept into the infrabuccal sac. Similarly, in excavating cavities in decaying stems or roots, and in malaxating sound or moribund plant tissues, the workers produce a finely divided vegetable débris—containing more or less numerous fragments of hyphæ—much of which is scraped into the infrabuccal chambers of the imagines.

The Fungivorous Habit among Formicidæ

The data presented in this paper reveal the fact that ants are closely associated with fungi, but they do not indicate that the Formicidæ, other than the Attii, are fungivorous.[1] The cropping of aerial hyphæ does not indicate necessarily that fungi are eaten by ants. Furthermore, the spores and fragments of mycelia, which occur so characteristically in the pellets of imagines, appear to be detritus, cleaned from the bodies and appendages of the ants, rather than food-residues. The more or less "pure cultures" of particular fungi in the ant-inhabited stems of *Cuviera* and *Plectronia,* the pseudobulbs of *Myrmecodia* and *Hydnophytum* and the carton nests of *Lasius fuliginosus* and *L. umbratus* cannot be considered to prove that the fungi are actually cultivated and eaten by the ants. Unless all fungi are equally resistant to continued cropping, and react similarly in the peculiar environmental conditions within the domatia, certain species are likely to become dominant. If a particular form does become dominant and grows actively, it will be likely to be transferred to new nests by the queens, since the infrabuccal sacs of imagines almost invariably contain more or less numerous fragments of hyphæ or spores.

Ants as Active Agents in the Dissemination of Fungi

That ants play an important rôle in the dissemination of disease has been suggested by Darling (1913), Wheeler (1914) and Studhalter and Ruggles (1915). Wheeler states in his paper upon "Ants and bees as carriers of pathogenic microorganisms":

> "It would seem to be possible, therefore, for ants to spread disease germs in three different ways: first, by simply walking over or into human food, as Darling has shown; second, by dropping into it infected hypopharyngeal pellets, and third, by contaminating it with their germ-laden feces."

As shown upon preceding pages, there is a general tendency among ants to take spores, fragments of mycelia and bits of decaying plant tissue into their infrabuccal pocket. In this sac the fungi become mixed with food-residues and mineral and vegetable detritus, forming a pellet which is subsequently voided upon any convenient surface. The composition of the infrabuccal pellet suggests that it is a "culture" or potential source of infection. Furthermore, von Ihering (1898), Huber (1905) and more recently Bruch (1919) have demonstrated that the hyphæ and spores in the voided pellets of Attiine queens actually are viable and give rise to luxuriant growths of hyphæ. In view of these facts, it seems probable that the Formicidæ are active agents in the dissemination of many of the higher fungi, particularly in tropical regions where ants are so numerous and ubiquitous.

---

[1] The pellets in the trophothylaces of Pseudomyrmine larvæ contain spores and fragments of hyphæ and a variety of miscellaneous substances, but we have been unable to determine how much of this material is actually eaten by the larvæ.

Origin of the Fungus-Growing and Fungus-Feeding Habits

There has been considerable speculation in regard to the origin of the highly specialized Attiine ants and of their remarkable fungus-growing and fungus-feeding habits. Von Ihering (1894) is of the opinion that the fungus-growing and leaf-cutting habits may have originated as a specialization from the seed-storing habit. Emery (1899) believes that the cropping of adventitious growths of hyphæ upon the walls of the domatia, "est vraisemblablement l'origine de la mycophagie exclusive des Attinæ." Forel (1902) considers that in the early stages of the development of the biocoenose, the fungus-gardens were grown upon insect excrement, and Wheeler (1907) cites the habits of fungicolous termites and ambrosia-beetles in support of this hypothesis. The latter investigator states: "the method employed by the *Atta* queens in manuring their incipient fungus-gardens suggests that the food plant may have been originally grown on fecal substances."

There are certain general tendencies in the relations between ants and fungi which are worth mentioning in this connection. Thus, there is a general tendency for queens, as for other imagines, to transport spores and fragments of hyphæ in their infrabuccal cavity. This is of interest in discussing the extraordinary habits of the Attiine queens. Furthermore, I have called attention to the fact that there are more or less "pure cultures" of adventitious fungi in the nests of certain ants, which grow with particular luxuriance in those regions of the domatia where the detritus (pellets, feces, etc.) of the colony is deposited. If such mats of aerial hyphæ were edible, it would be a simple matter for the ants to increase the volume of their primitive fungus-gardens by adding extraneous materials, *i.e.*, insect excrement, vegetable débris, etc., to the original compost.

In conclusion, it is to be emphasized that my observations are based upon the study of specimens preserved in alcohol and, therefore, will have to be verified by experimentation with living organisms. However, they reveal a very general and close association between ants and fungi, and emphasize the necessity for further and more detailed investigations upon the structure and feeding habits of Formicidæ and the rôle of these insects in the dissemination of plant diseases.

The ants used in this investigation were obtained from the extensive collections of my colleague, Professor W. M. Wheeler, and have been carefully identified by him.

LITERATURE CITED

Adlerz, G.
'86 Myrmecologiska Studier. II Svenska Myror och deras Lefnadsförhållanden. K. Svensk. Vetensk. Akad. Handl. Bihang. 11: 1–329.

Belt, T.
'74 The Naturalist in Nicaragua. London.
Brants, A.
'41 Bijdrage tot de kennis der monddeelen van eenige vliesvleugalige gekorvenen (insecta hymenoptera). Tijdschr. Natuurl. Geschiedenis Phys. 8: 71–126.
Bruch, C.
'19 Nidos y costumbres de hormigas. Rev. Soc. Argent. Cienc. Nat. 4: 579–581.
Darling, S. F.
'13 The Part Played by Flies and Other Insects in the Spread of Infectious Diseases in the Tropics, etc. Trans. 15th Internat. Cong. Hyg. Demogr. Sect. V. Washington.
Donisthorpe, H. St. J. K.
'15 British Ants, Their Life-history and Classification. Plymouth, England.
Elliott, J. S. Bayliss.
'14 Fungi in the Nest of Ants. Trans. Brit. Mycol. Soc. 138–142.
Emery, M. C.
'99 Végétarianisme chez les fourmis. Arch. Sci. Phys. Nat. 8: 488–490.
'12 Alcune esperienze sulle formiche granivore. Rend. Sess. R. Acad. Sci. 1st. Bologna. 16: 107–117.
Farquharson, C. O.
'14 Correspondence in Proc. Ent. Soc. London. Pages XLII–XLVII.
Ferdinandsen, C., and Winge, O.
'08 Fungi from the Danish West Indies collected 1905–1906. Bot. Tidsskr. 29: 1–25.
Forel, A.
'02 Beispiele phylogenetischer Wirkungen und Rückwirkungen bei den Instinkten und dem Körperbau der Ameisen als Belege für die Evolutionslehre und die phychophysische Identitätslehre. Jour. Psychol. Neurol. 1: 99–110.
Huber, J.
'05 Ueber die Koloniengründung bei *Atta sexdens.* Biol. Centbl. 25: 606–619, 625–635.
Ihering, H. von.
'94 Die Ameisen von Rio do Sul. Berlin. Ent. Ztschr. 39: 321–446.
'98 Die Anlage neuer Colonien und Pilzgärten bei *Atta sexdens.* Zool. Anz. 21: 238–245.
Janet, C.
'95*a* Étude sur les Fourmis. 8. Sur l'Organe de nettoyage tibio-tarsien de *Myrmica rubra* L., race *levinodis* Nyl. Ann. Soc. Ent. France. 63: 691–704.
'95*b* Études sur les Fourmis, les Guêpes et les Abeilles. 9. Sur *Vespa crabro* L. Mém. Soc. Zool. France. 8: 1–140.
'96 Les Fourmis. Bull. Soc. Zool. France. 21: 60–93.
'97 Études sur les Fourmis, les Guêpes et les Abeilles. 13. Sur le *Lasus mixtus.* Limoges. 1–62.
Lagerheim, G.
'00 Ueber *Lasius fuliginosus* (Latr.) und sein Pilzzucht. Ent. Tidskr. 21: 17–29.
Lubbock, Sir John.
'77 On Some Points in the Anatomy of Ants. Monthly Micros. Jour. 18: 121–142.
Meinert, F.
'60 Bidrag til de danske Myrers Naturhistorie. K. Dansk. Vidensk. Solsk. Skr. 5: 275–340.

Miehe, H.

'11 Javanische Studien II. Untersuchungen über die Javanische Myrmecodia. Abhandl. Math. Phys. Cl. K. Sächs. Gesell. Wiss. 32: 312–361.

Moeller, A.

'93 Die Pilzgärten einiger südamerikanischer Ameisen. Schimper's Bot. Mitt. aus d. Tropen. IV: 1–127.

Moggridge, J. T.

'73 Harvesting Ants and Trap-door Spiders. London.

Müller, Fritz.

'74 The Habits of Various Insects. (Letter to Darwin). Nature 10: 102–103.

Perkins, R. C. L.

'14 Correspondence in Proc. Ent. Soc. London. Pages XLV, XLIX.

Studhalter, R. A., and Ruggles, A. G.

'15 Insects as Carriers of the Chestnut Blight Fungus. Penn. Dept. For. Bull. 12: 1–33.

Tanner, J. E.

'92 *Œcodoma cephalotes.* Jour. Trinidad Field Nat. Club. 1: 68–69, 123–127.

Wheeler, W. M.

'07 The Fungus-growing Ants of North America. Bull. Amer. Mus. Nat. Hist. 23: 669–807.

'14 Ants and Bees as Carriers of Pathogenic Microorganisms. Amer. Journ. Trop. Dis. Prev. Med. 2: 160–168.

DESCRIPTION OF PLATES

Plate VI

Fig. 1. *Cuviera species.* Section of "fungus-garden" and medullary substratum. × 160.

Fig. 2. Portion of infrabuccal pellet of *Crematogaster impressiceps* var. *frontalis.* This pellet was composed entirely of the ambrosia-like fungus. × 400.

Fig. 3. *Cuviera angolensis.* Section of the wall of a recently occupied myrmecodomatium, showing aerial hyphæ. × 210.

Fig. 4. Portion of an infrabuccal pellet of *Pachysima aethiops,* showing aerial hyphæ, spores and other detritus. × 330.

Fig. 5. Portion of a larval pellet of *Pachysima aethiops.* Spores resting upon a ground mass of coccid tissue. × 180.

Fig. 6. Portion of a larval pellet of *Pseudomyrma gracilis* (var. nov.), showing pollen and fragments of insect. × 58.

Plate VII

Fig. 7. Portion of an infrabuccal pellet of *Pseudomyrma gracilis* var. *mexicana,* showing pollen and various types of spores. × 330.

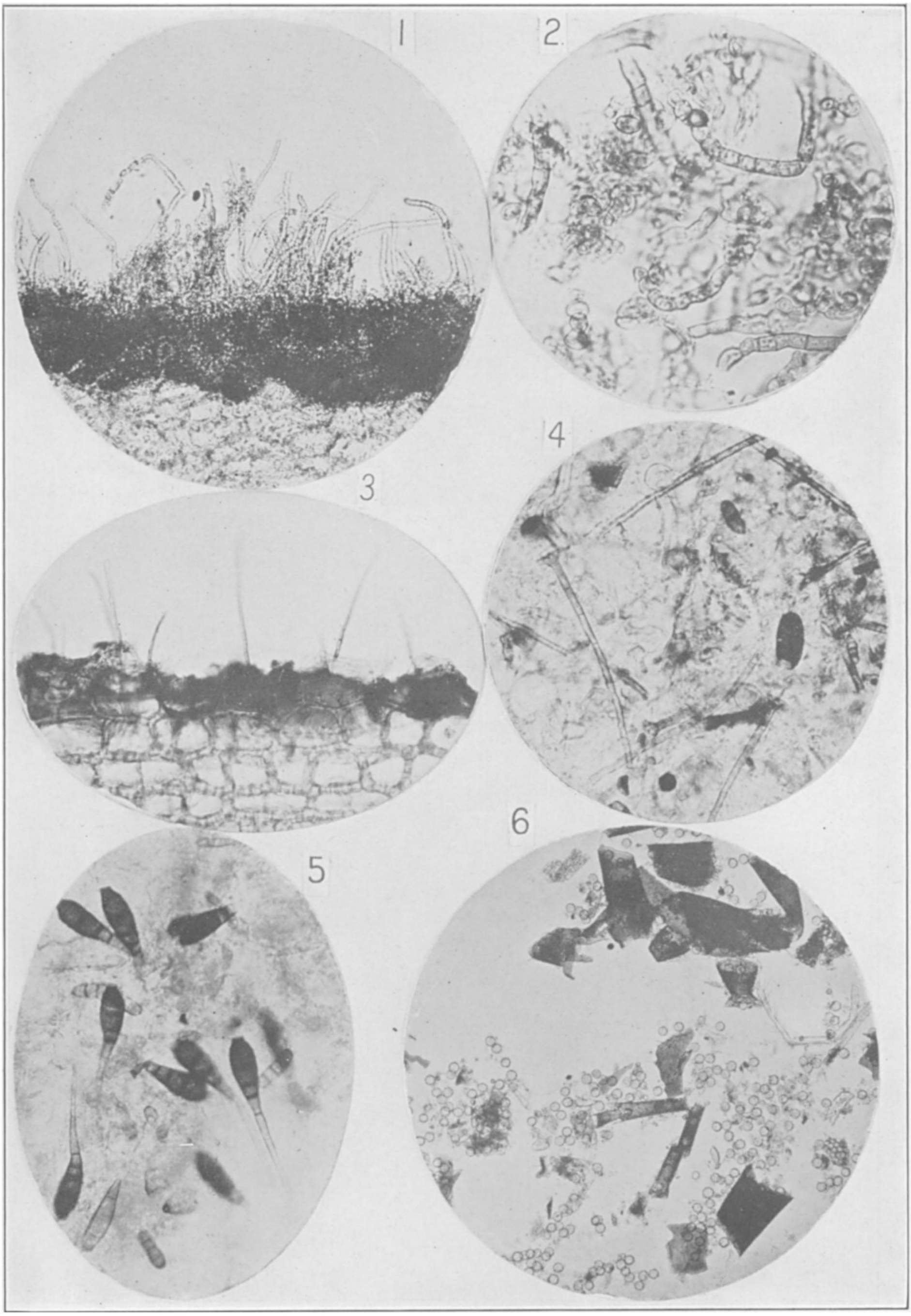
Fig. 8. Portion of an infrabuccal pellet of *Pseudomyrma decipiens.* This pellet was composed entirely of small, light colored spores. × 330.

Fig. 9. Portion of a larval pellet of *Pseudomyrma flavidula,* showing mixture of soft insect tissue and spores of various types. × 78.

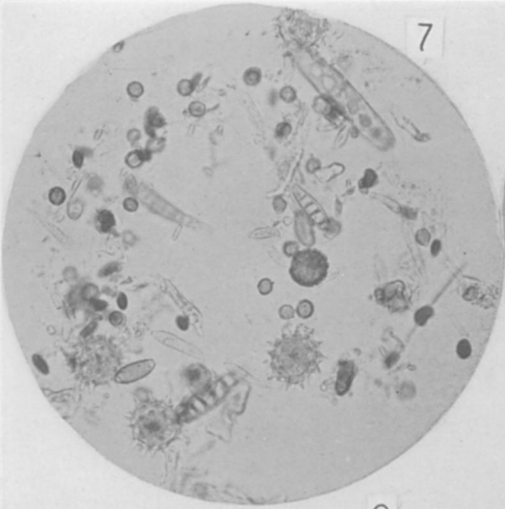
Fig. 10. Portion of an infrabuccal pellet of *Pseudomyrma flavidula,* showing numerous hyphæ. × 330.

Fig. 11. Portion of an infrabuccal pellet of *Pseudomyrma flavidula* var. *delicatula,* showing various types of spores. × 330.

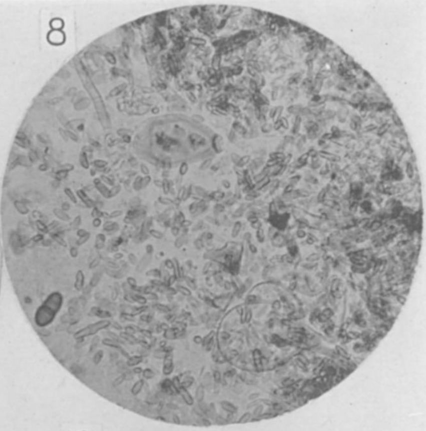
Fig. 12. Portion of an infrabuccal pellet of *Atta cephalotes,* showing vegetable débris and dirt. × 205.



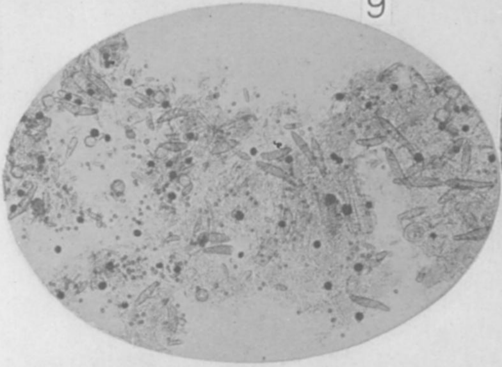
Bailey on Ants and Fungi.



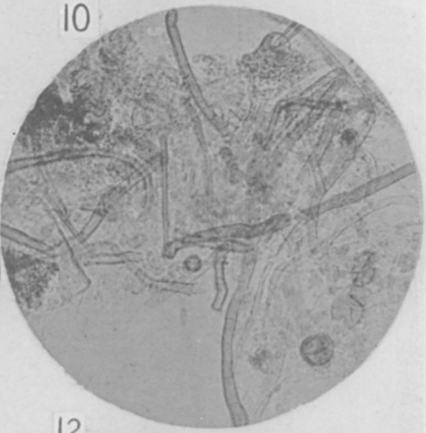
7



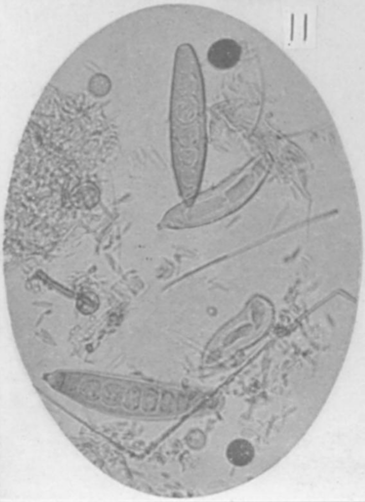
8



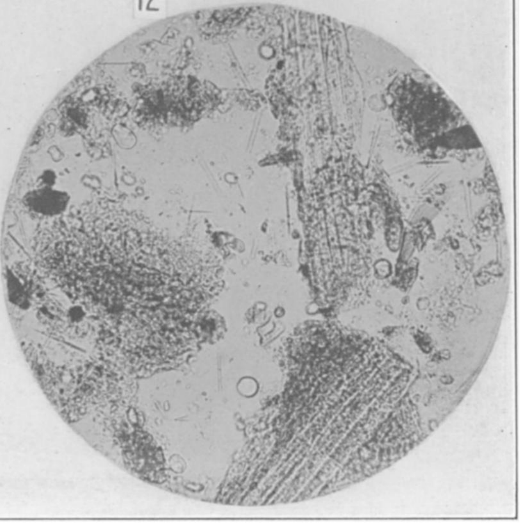
9



10

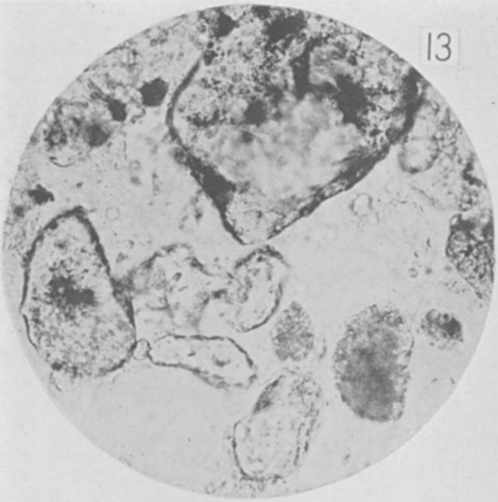


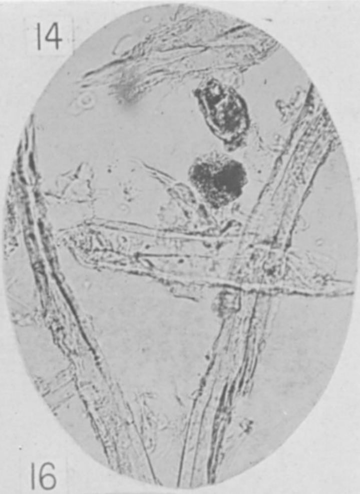
11

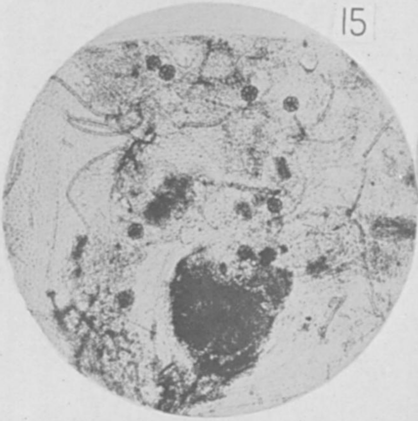


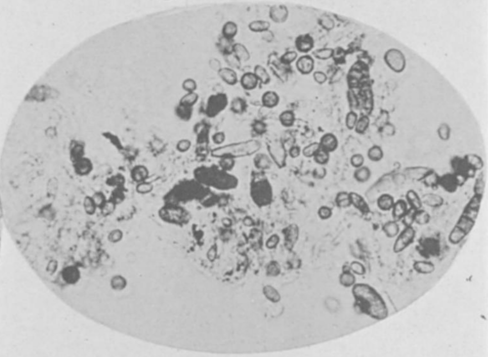
12

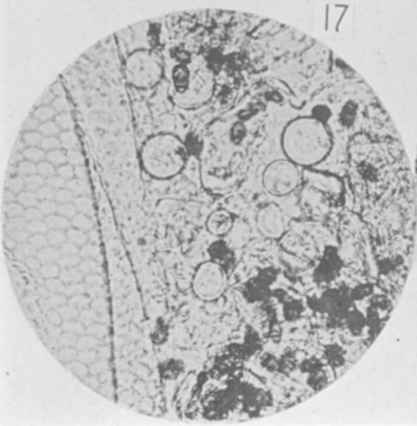
BAILEY ON ANTS AND FUNGI.

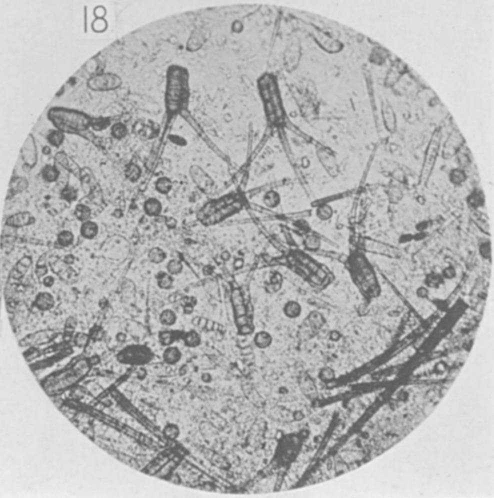

13


14


15


16


17


18

BAILEY ON ANTS AND FUNGI.

Plate VIII

Fig. 13. Portion of an infrabuccal pellet of *Pogonomyrmex barbatus* var. ***marfensis,*** showing sand. × 322.

Fig. 14. Portion of an infrabuccal pellet of *Camponotus herculeanus* subsp. ***ligniperda*** var. *novaboracensis.* This pellet was composed entirely of the shredded wood of *Thuja occidentalis.* × 205.

Fig. 15. Portion of an infrabuccal sac of *Camponotus brutus,* containing spores, hyphæ and bits of decaying plant tissue. × 105.

Fig. 16. Portion of an infrabuccal pellet of *Diacamma australe.* This pellet was composed largely of spores. × 390.

Fig. 17. Portion of an infrabuccal sac of *Camponotus abdominalis* var. *costaricensis,* containing numerous spores and pollen. Note texture of membranous sac on left. × 322.

Fig. 18. Portion of an infrabuccal pellet of *Odontomachus haematoda,* showing great numbers of spores of different types, hairs, and dirt. × 205.